THE LIFE-HISTORY OF A BEE-FLY (SPOGOSTYLUM ANALE SAY) PARASITE OF THE LARVA OF A TIGER BEETLE (CICINDELA SCUTELLARIS SAY VAR. LECONTEI HALD.).

By Victor E. Shelford.

I. Introduction.

The life histories of the American Bombyliidæ are imperfectly known and this lack of knowledge is due largely to the difficulty of studying parasitic forms. The species in question is never abundant and consequently much time has been consumed in getting together the data for the account here presented. Near Chicago it occurs on dry sandy places where there is much vegetation and where the sand is slightly blackened with humus. The data presented were collected mainly in connection with work upon the host which involved collecting and rearing to maturity about a thousand host larvæ.

The larva of the parasite was first discovered in 1904 but none was successfully reared until 1906; the method of egg laying was not successfully observed until 1908 and 1909 while attempts to study the adult habits in 1910 and 1911 were only partially successful.

Life History of the Host.

Cicindela scutellaris Say *var. Lecontei* Hald. is found in areas of dry sand to which considerable humus has been added by decaying vegetation (Wickham '02, Shelford '07, '11). Adults are present near Chicago from April to June and again in September. The fall individuals are those emerging from the pupal stage and are not sexually mature. These individuals pass the winter in the ground, become sexually mature after the warm days in April and deposit eggs in May and early June.

The young larvæ appear in late May and early June. The larvæ live in vertical burrows which end at the surface in a smooth circular opening (Fig. 2; also bh of Fig. 16, p. 221). They pass through three instars, the first two of which are about one month each in duration. The third and last stage is reached in the last part of July, in August and early September. These stages pass the winter in the burrows, appearing at the surface in May, and feeding until from June 20 to July 20. Each larva then digs a pupal (pch of Fig. 16, p. 221) burrow filling the main burrow at the same time. The larva remains quiet in this cavity for about three weeks when it pupates if it has not been parasitized, and emerges in August, making its way to the surface about three weeks later.

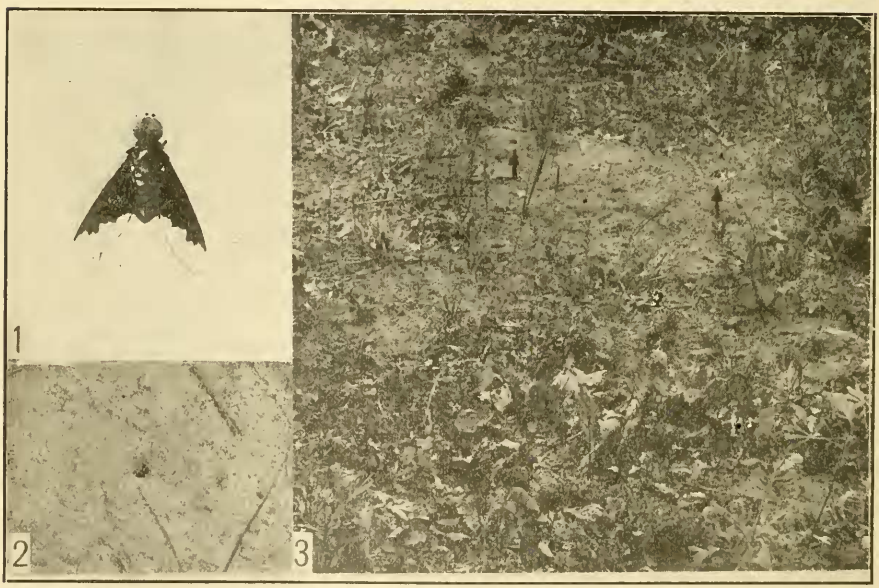


Fig. 1. The adult fly about twice natural size.
Fig. 2. A burrow of a larva of the second instar of *C. scutellaris Lecontei*, about natural size.
Fig. 3. General habitat of *C. scutellaris Lecontei* at a point where the fly was observed ovipositing, and the kind of situation in which the parasite is most abundant. The burrows of two larvæ of the host are in the last instar, and are visible above the small arrows.

II. Life History of the Parasite (*Spogostylum*).

1. Adult Habits.

The adult is a bright shiny velvet black fly with the basal two thirds of the wings black and the distal third transparent. (Fig. 1). It occurs in July and August, in open spots on sandy soil, especially in the kinds of situation shown in Fig. 3, where herbaceous vegetation and flowers are numerous. It is commonly associated with other bee flies such as *Anthrax impiger* Coq., *Anthrax fulvohirta* Weid., and *Anthrax molitor* Loew. which are much more abundant and often visit flowers in numbers, also *Exoprosopa*, which probably lays in the burrows of the *Bembecid* wasps. The habits of the male *Spogostylum* have not been observed. The female usually alights near the ground on the lowest plants or on sticks and leaves. In sunny weather she starts with remarkable swiftness when a shadow is passed over her but appears not to be stimulated by the presence of the observer under other conditions. In cloudy weather the writer has shaken an insect net within a few inches of one of the flies without causing her to move. The food habits have not been observed but a single individual lapped sugar and water from a piece of paper, while in captivity.

2. Egg Laying.

The female flies about two inches above the clear open sand in an irregular somewhat zig-zag fashion until apparently by chance its eyes pass above a hole in the sand, (Figs. 2 and 3). When this happens, the fly suddenly halts and moves backward and downward in a curved course. At the same time the abdomen is thrust forward so that it touches the surface of the sand at a point 5 to 10 mm. from the edge of the hole. The impact of the abdomen upon the sand is sufficient to perceptibly move small particles, some of which appear to fall in the burrow. The thrusts are usually repeated a number of times. After each movement, the fly returns to approximately the position at which the thrust began. The sight of the hole below the eyes acts as a trigger which sets off the thrusting reflex. The host larvæ frequently rest in the burrow some distance below the surface. On two occasions the fly stopped thrusting when the larva appeared near the surface. The size and shape of the hole appear not to be of prime importance.

Burrows of the second instar of *Cicindela* are most frequently visited. This is probably due to the fact that these holes are most abundant. The burrows of young spiders (*Geolycosa*) which have a web around the opening, are not rejected while holes of the first and third instars of *Cicindela* as well as partially covered holes produce the reaction at least once. General results of one observation are shown in table I.

TABLE I.

A Seven Minute Observation of the Egg Laying Reaction of a Female *Spogostylum*, July 16, 10:30 a. m.

Hole Producing Reflex	Stage	No. of Thrusts	Remarks
Burrow of— C. Lecontei	2 d.	7	Larva appeared.
Geolycosa	young	3–5	Web surrounding opening.
Large nondescript hole	...	...	Rejected after halt without thrust
Burrow of— C. Lecontei	2 d.	6	Stick half covering hole.
C. Lecontei	2 d.	2	Burrow less than one cm. deep due to closing near surface; probably during moult.
C. Lecontei	1st	2	
C. Lecontei	2 d.	5	Stick across hole.
C. Lecontei	3 d.	3–5	Partially covered.

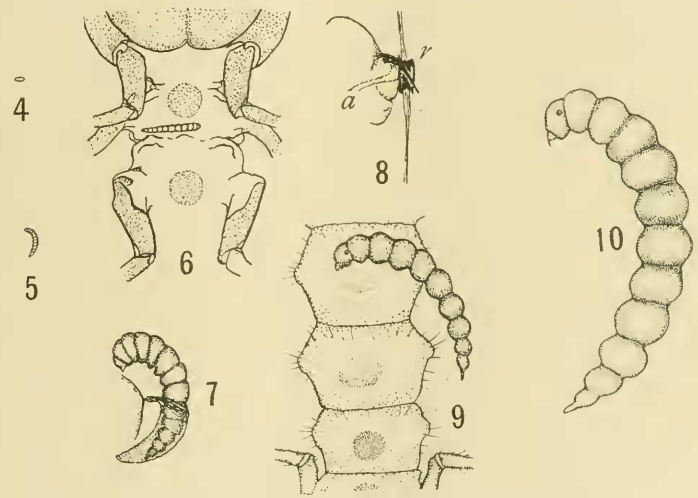
A summary of the observation of egg laying is as follows: Egg laying thrusts were executed, by two individuals observed, before holes as follows: One first larval stage of the host, eighteen second larval stages including one partially covered with a stick, and a shallow one (filled below the surface); one third stage of Cicindela, one small spider hole. One large nondescript hole arrested the flight but did not produce the egg laying thrust.

3. Egg, (Fig. 4).

A female taken while laying was found to contain a very large number of eggs, which could be squeezed out by a gentle pressure upon the abdomen. The eggs are light brown ellipsoids .28 mm. by .12 mm. They are not adhesive.

4. Larva (Fig. 5).

Young larvæ are most commonly found singly on the ventral side of the thorax of host larvæ of the third instar, where they cling between the legs. No second instars have been found with parasites. While in the position between the legs they cannot be reached by the host and do not come readily into contact with the sides of its burrow. There are however frequent exceptions to this, for host larvæ not infrequently have more than one larva between the legs or single larvæ on other parts of the body. One host larva had in addition to the parasite on the ventral side of the throax, two others on the posterior third of the abdomen. Attempts to secure eggs or young larvæ from sand gathered from the edges of burrows about which eggs had been laid or to rear larva from eggs squeezed from a laying female, have failed. Neither have we



Figures 4–10. Early larval stages of *Spogostylum anale* Say.

Fig. 4. The egg; enlarged about five diameters.
Fig. 5. A young larva of the second stage; about five times natural size, in a somehwat curved position.
Fig. 6. The same in position enlarged about nine times.
Fig. 7. At the time of moving to the abdomen; enlarged about five times. The larva has withdrawn its anterior half from the old integument.
Fig. 8. The larva in position in the thorax, showing the ring of thickened chitin(r) in the integument of the host and the long slender mandibles in position.
Fig. 9. The larva after one day on the abdomen of the host: about five times natural size.
Fig. 10. The larva at the end of the second day upon the abdomen.

discovered how the larva reaches the body of the host. The host larva with the three parasites was placed in a tube of sand one inch in diameter together with two other host larvæ, one bearing two parasites and the other uninfested. The double and triple infested hosts died leaving five parasitic larvæ in the tube with the one live host larva. *None* of the parasites *reached the host larva*. Host larvæ dug from the point where a female fly was seen to deposit eggs on July 16 had parasites of the first and second instars on the ventral thorax when removed from their burrows Sept. 23d. About 7 percent of the host larvae are parasitized. While some catches of fifty host larvae were as high as 16 percent infested others were quite free from parasites. This is particularly true in the pine area (see p. 222), where only one out of several hundred host larvae were parasitized.

The structure of the larva was but little studied on account of lack of material. The head segment bears the usual mandibles, which are long and curved. They pierce the integument of the host obliquely; a ring of thickened chitin develops about them and the mouth is brought into contact with the center of the ring and thus with the tissues and fluids of the body (Fig. 8). The number of larval moults has not been fully determined and the following account is not necessarily accurate. The smallest larvæ found are from 0.5 to 0.6 mm. in length and are evidently in the first instar. These were taken in late summer and autumn and occasionally in spring. Most of these larvæ moult in the fall; all pass the winter attached to the body of the host, those of the first stage moulting in early May. When the larva moults, the integument splits in the region of the thorax. The anterior end of the body is withdrawn from the old skeletal parts, leaving the old mandibular skeleton imbedded in the host. The posterior part of the larva apparently remains in the old integument until the new integument of the head region is hardened when a new attachment to the host is affected. When again attached, the larva withdraws the abdomen from the exuvium (Figs. 5, 6 and 7).

The larvæ of the second instar, (length 1.2 to 1.6 mm.), probably moult again after the host has fed about a month (early June), but this is not certain because exact measurements could not be made of the small living larvæ while attached to the host and they could not be removed without killing them.

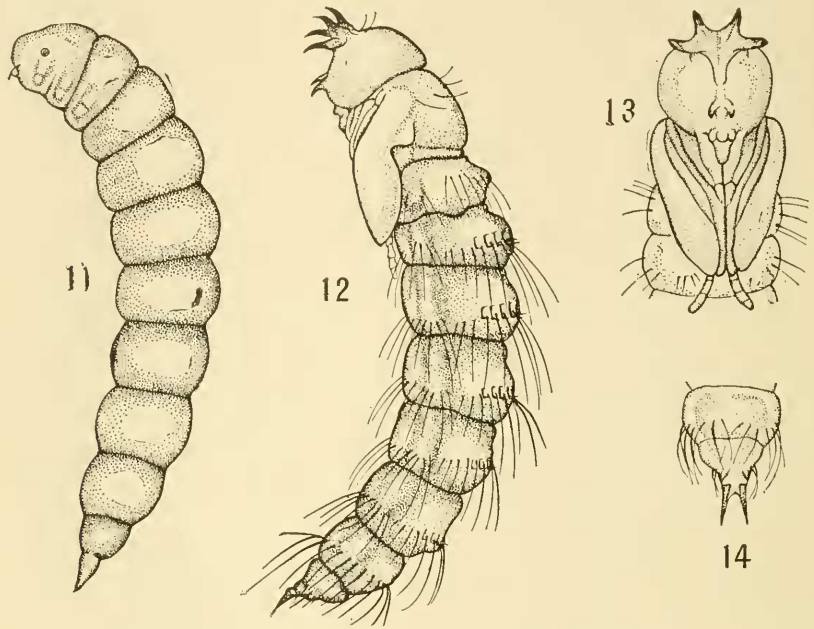
A third moult takes place about the time the host stops feeding (late June), but in the cases observed, before the pupal cell is constructed. This moult clearly takes place but the larva again could not be accurately measured.

In late June the host constructs the pupal cell (*pch of Fig. 16, p 221*) and becomes relatively inactive but does not normally pupate for a month. The parasite does not grow rapidly until the host has been in the pupal cell for about three weeks. By this time the old organs of the host have for the most part, broken down and the internal parts are in a semifluid condition. The parasitic larva now moults again and this time leaves its former position completely. In the four or five cases observed it moved to about the middle of the ventral side of the host, (Fig. 9). It will be noted that at the time of the previous moults of the parasite the host was active and if the larvæ had completely released its hold at any of these times the result would probably have been its own destruction. At the time of this fourth moult, on the other hand, the host is almost unable to move. Immediately upon securing the new source of food through the abdomen of the host the parasite begins to grow more rapidly and more than doubles its length in 48 hours. The length at the time of the fourth moult is about 4.5 mm.; after 24 hours the length is 6.5 mm. (Fig. 9), and during the next 24 hours the larva reaches a length of 1 cm. (Fig. 10), which is two-thirds the length of the abdomen of the host. At the end of 144 hours the parasitic larva is full grown (Fig. 11). The length is now 1.8 cm. and all of the later rapid growth has apparently taken place without further moulting. The full grown larva passes six or seven days in the pupal cavity of the host in a quiescent stage before the pupal moult occurs.

5. Pupa and Adult.

The pupa is of the type common among the diptera. There are four curved hooks upon the anterior side of the head united at the base in the form of a fan (Figs. 12 and 13). Two smaller hooks on the ventral side of the head appear to correspond in position to the antennæ. There is a circle of long stiff bristles on each segment of the abdomen together with U shaped bristles on the dorsal side. The pupa upon emerging is unpigmented; the hooks on the head become dark in about five days; the head becomes light brown in nine days and dark

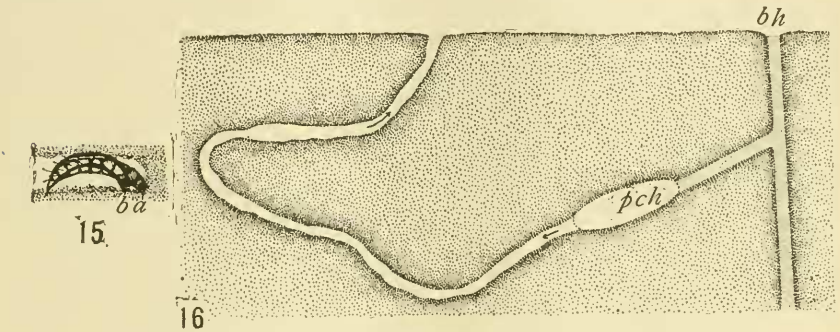
brown in thirteen days; pigment appears in the wings at the end of thirteen days in the center of the segments of the abdomen in two weeks. Pigmentation is apparently complete in about sixteen to eighteen days (July 13 to Aug. 3).



Figures 11–14. Late larvæ and pupal stages.
Fig. 11. Full grown larva showing the leg buds; enlarged five times.
Fig. 12. Side view of the pupa; enlarged five times.
Fig. 13. Front view of the anterior end of a fly pupa.
Fig. 14. Front view of the posterior end of the same.

Some time soon after the pigment is completely developed, the pupa begins to use the hooks for digging. In this process the numerous long stiff bristles arranged in a ring about the segments and projecting backward are of much importance for they tend to make simple movements either push the body forward or push loose sand backward. The large U-shaped bristles along the dorsal side may or may not function in this way also. The main digging operations are carried on by means of the hooks on the head. The two spines of the posterior end serve as anchoring organs. The body is curved dorsalward in the form of a bow with the dorsal side pressed against the upper side of the burrow. The U-shaped bristles prominent upon the dorsal side may function as anchors in this

operation. The two posterior spines are thrust into the floor of the burrow and the curvature is increased, which cause the head to move back as shown in Fig. 15. After a number of hoeing movements, the pupa usually wriggles backward carrying the sand with it by means of the bristles and again wriggles forward until the head is in contact with the end of the burrow. The hoeing movement is repeated or less frequently the body is rotated, the hooks serving as a boring organ.



Figures 15–16. Emergence from the ground.

Fig. 15. Diagram showing the movement of the pupa in digging its way out of the ground. Natural size (a).

Fig. 16. Showing the burrow and pupal cell of the host with the path dug by the pupa of Spogostylum.

The boring movement was observed in the case of one individual, the host of which had been confined in a glass tube eight inches long and one and one-half inches in diameter. The burrow and pupal cell of the host were constructed in contact with the glass. Much of the life history of one parasite was thus observed. The digging of the parasite pupa began at night, and was not noted until the middle of the next forenoon (July 15), [began in pch of Fig. 16, p. 221]. During the last eight hours the larva progressed at the rate of 1 cm. per hour. It moved in contact with the glass and traveled more than once around the tube just inside the glass. The total distance through which the parasite dug was about 24 cm. Apparently immediately upon reaching the surface the fly emerged. It left the pupal integument sticking in the burrow. The emergence of the fly was not observed as the last centimeter of digging was accomplished in less than 20 minutes and the fly emerged between observations. The adult was found resting on a small blade of grass near the hole. This adult lived only about two days.

A pupa removed to a watch glass with the bottom covered with moist filter paper executed the digging movements for a day or more, but failed to emerge. One reared in a very small amount of sand and between two glass plates dug to the surface and then back into the sand again. It emerged in imperfect condition within the sand.

III. Other Species.

Work on the European species of the family Bombyliidæ is also far from extensive. Dufour gave an account of the larvæ, pupæ, and adult habit of *Bombylius major*. He found this species in March 1857 on the sloping banks of sand hills with southern exposure. He saw the fly light quickly at the openings of the burrows of Hymenoptera. In the locality, the burrowing hymenoptera were principally Andrenidæ and especially *Colletes hirta*. Dufour was never able however to find the egg of the fly. Williston '08, p. 213, summarizes the known hosts of the Bombylidæ. In connection with the study of *Spogostylum anale* (July 30), *Anthrox impiger* was seen resting on the ground touching the abdomen to the surface of the sand. *Anthrax impiger* Coq. (July 16–30), lights on blossoms of horse mint, etc. or rests on other objects on the ground. Two, a pair, of *Exoprosopa fascipennis* Say were taken while flitting before a burrow of *Microbembex monodonta*.

IV. Ecological and Geographic Distribution.

1. Ecological Distribution of Parasite and Host.

Near Chicago, the fly larvæ appear to be confined to *C. Lecontei*. One or two larvæ of *C. hirticollis* which do not occur with those of *C. Lecontei* were found to bear similar parasites. Adults of *Spogostylum* have never been seen near the *C. hirticollis* habitat. *C. purpurea limbalis* which lives on steep clay bluffs is parasitized by a larvæ somewhat different from that of *Spogostylum*.

In 1907 and 1912 I pointed out that the development of vegetation upon the sand areas at the head of Lake Michigan takes places in an orderly fashion. Cottonwoods are the pioneers and are accompanied by *Cicindela lepida*. Only one *Spogostylum anale* Say has been seen in these localities and this when a strong wind was blowing from a more favorable habitat. The cottonwoods are succeeded by pines and *Spogostylum* is rare among them. *Cicindela formosa generosa* occurs in the

mixed pine and cottonwood areas but none of these have been found with parasites. The large pit and goose-neck burrow probably prevent this species from serving as a host (Shelford, '08). Very few parasitized *Cicindela Leconti* larvæ have been taken here though the host is only a little less abundant than in the oak area. It is on the margins of the depressions in the pine areas that the larvæ of *C. tranquebarica* Hbst. are numerous (Shelford '07) but none of those of this species were found parasitized, though the number of larvæ dug was great.

Spogostylum anale and its host species are most abundant in the early stages of the black oak forest where cacti occur (Fig. 3). The exact landscape aspect is significant only as an index of the physicial conditions. The evaporation in these open oak forests is about one half that of the cottonwood area and less than that of the pine area. The available soil moisture is less (Shelford, '12).

2. Geographic Distribution.

American dipterologists have kindly supplied me with data on the distribution of *Spogostylum anale* as follows:

Prof. D. W. Coquillett: Sandy Hook, N. J.; Indiana; Carbondale, Ill.; Mississippi; British Columbia; Washington; Mesilla, N. M.; St. Louis, Mo.; Shreveport, La.; Georgia; Enterprise, Fla.; Cambridge, Mass.

Dr. J. S. Hine: Mission, British Columbia; Onaga, Kansas; Akron, Ohio; Cincinnati, Ohio.

Dr. C. T. Brues: Douglas Co., Kansas; Crete, Nebr.; Austin, Texas.

Dr. C. F. Adams: Jackson Co., Mo.; Lawrence, Kan.; Clark Co., Kan.; Fayetteville, Ark.

Prof. E. P. Felt: South Britian, Conn.; Albany, N. Y.

Prof. J. H. Comstock: Manlius, N. Y.

Dr. A. L. Meander: Galveston, Texas; Golden, Colo.

Map (Fig. 17) shows the distribution area of the host (A) generously represented by connecting the more remote localities along nearly direct lines where suitable habitats are known to occur. The distribution of the parasite is wider than that of the host species including all varieties extending into Mexico and along the Pacific coast. Accordingly the parasite must use another host. Several other species of the tiger beetles may no doubt serve this purpose.

Some of the flies reared in a hot green house lacked the white hairs along the abdomen, which characterize the species. Prof. Williston tells me that these hairs were absent from specimens taken in Mexico and doubtfully referred to this species by Osten Sacken.

Fig. 17. Showing the distribution area of the host species. (A of the legend.) The area blocked out is generous including all the probable territory. The crosses (B of the legend) represent state and country records. The round dots (C of the legend) represent some of the definite localities from which the fly has been recorded.

V. Summary.

1. The adult fly deposits eggs at the edge of circular openings in sand. In the areas inhabited by the flies (near Chicago) these openings are usually the larval burrows of *C. scutellaris Lecontei* Hald. p 215.

2. The sight of the burrow opening, beneath the eyes appears to call forth the egg laying reflex, p. 215.

3. The larvæ live as ectoparasites upon the tiger beetle larvæ for a little less than one year, growing slowly and moulting several times, p. 217.

4. When the host is ready to pupate, the larva moults, moves to the abdomen and grows to adult size in about six days, p. 219.

5. When the pupa is fully mature it digs out by means of hooks on its head and backward projecting bristles on the abdomen. The digging is sometimes downward for a time and lasts for more than 24 hours, p. 221.

6. The parasite is more widely distributed than its host, p. 223.

VI. Acknowledgments and Bibliography.

The writer is indebted to Dr. S. W. Williston and Mr. C. A. Hart for the identification of the Bombyliidæ, and to the gentlemen named above for the distribution records.

Aldrich, J. M. A Catalogue of North America Diptera. Smithsonian Miscl. Coll. Vol. XLVI, (No. 1444). Cites work on life histories.

Dufour, Leon. '58. Histoire des Metamosphoses du Bombylius major. Ann. Soc. Ent. Ser. 3. Tome. 6. pp. 503–511, pl. 13–111. Fig. 1–9.

Shelford, V. E. '07. Preliminary Note on the Distribution of the Tiger Beetles and its Relation to Plant Succession. Biol. Bull. Vol. XIV, pp. 9–24.

Shelford, V. E. '08. Life histories and Larval Habits of the Tiger Beetles. Linn. Soc'y's Journal Zoology, Vol. 30, pp. 157–184.

Shelford, V. E. '12. Ecological Succession IV. Vegetation and the Control of Animal Communities. Biol. Bull. XXIII, pp. 59–99.

Townsend, C. H. T. '93. The Pupa of Argyramœba œdipus Fabr. (Spogostylum). Am. Nat. Vol. XXVII. No. 313, pp. 60–63. Jan., 1893.

Wickham, H. T. '02. Habits of North American Cicindelidæ. Proc. Davenport Ac. of Nat. Sci., Vol. 7, pp. 206–228.

Williston, S. W. '08. Manual of North American Diptera. New Haven.